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Abstract: Nestedness refers to the structural property of complex networks that the neighborhood of a given node is a subset of the neighborhoods of better-connected nodes. Following the seminal work by Patterson and Atmar (1986), ecologists have been long interested in revealing the configuration of maximal nestedness of spatial and interaction matrices of ecological communities. In ecology, the BINMATNEST genetic algorithm can be considered as the state-of-the-art approach for this task. On the other hand, the fitness-complexity ranking algorithm has been recently introduced in the economic complexity literature with the original goal to rank countries and products in World Trade export networks. Here, by bringing together quantitative methods from ecology and economic complexity, we show that the fitness-complexity algorithm is highly effective in the nestedness maximization task. More specifically, it generates matrices that are more nested than the optimal ones by BINMATNEST for 61.27% of the analyzed mutualistic networks. Our findings on ecological and World Trade data suggest that beyond its applications in economic complexity, the fitness-complexity algorithm has the potential to become a standard tool in nestedness analysis.

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Article

Nestedness maximization in complex networks through the fitness-complexity algorithm

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Abstract: Nestedness refers to the structural property of complex networks that the rows and columns of the adjacency matrix can be sorted in such a way that the resulting matrix exhibits an upper-triangular shape. Following the seminal work by Patterson and Atmar (1986), ecologists have been long interested in revealing the configuration of maximal nestedness of spatial and interaction matrices of ecological communities. In ecology, the BINMATNEST genetic algorithm can be considered as the state-of-the-art approach for this task. On the other hand, the fitness-complexity ranking algorithm has been recently introduced in the economic complexity literature with the original goal to rank countries and products in World Trade export networks. Here, by bringing together quantitative methods from ecology and economic complexity, we show that the fitness-complexity algorithm is highly effective in the nestedness maximization task. More specifically, it generates matrices that exhibit a lower nestedness temperature than the optimal ones by BINMATNEST for 66.90% of the analyzed mutualistic networks. Our findings suggest that beyond its applications in economic complexity, the fitness-complexity algorithm has the potential to become a standard tool in nestedness analysis.

Keywords: Economic Fitness, Fitness-Complexity, Genetic algorithms, Nestedness temperature, Ecological networks.

1. Introduction

Network representations of complex interacting systems provide simple and powerful frameworks to characterize the topology of interactions and understand its impact on the emergence of collective phenomena [1,2]. Some topological properties are found in a wide variety of real networks, which has led scholars to investigate possible interaction mechanisms behind their emergence. An example is the heavy-tailed distribution of the number of links per node (degree): its ubiquity has motivated the study of various network growth mechanisms that can generate networks with that property [2]. First conceived [3] and measured [4,5] in biogeographic studies, *nestedness* [6] is one of such pervasive properties. In a perfectly nested network, the interaction partners of a given node are also partners of more generalist nodes. This property results in a upper-triangular shape of the adjacency matrix (see Fig. 1).

While perfectly nested networks are unambiguously defined, they are also rarely found in real systems. However, many real networks exhibit a high degree of nestedness, which means that their adjacency matrices can be ordered in such a way that they are almost perfectly upper-triangular. Based on various metrics, nestedness has indeed been found in systems as diverse as spatial patterns of species distribution [4,6], mutualistic plant-animal networks [7], manufacturer-contractor networks [8,9], country-product export networks [10,11], spatial patterns of firm distribution [10,12], among others. The ubiquity of the pattern has naturally led scholars to investigate how nestedness relates to other network properties [13–15], which mechanisms can possibly explain its emergence in ecological [16–18] and socio-economic [8,19,19] networks, and its implications for the stability and feasibility of ecological systems [20,21].

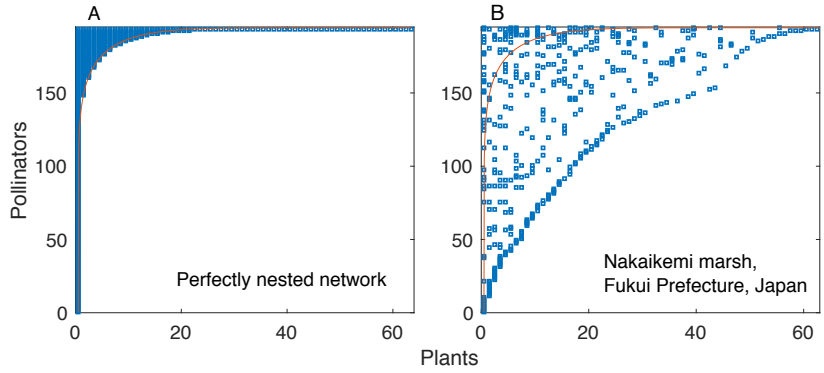

Figure 1. An illustration of the matrix of a perfectly nested networks as compared to the adjacency matrix of a non-nested network (Nakaikemi marsh pollination network) composed of the same number of nodes and links. In a perfectly nested network (left panel), one can define a isocline that perfectly partitions the matrix into a filled region (i.e., the region above the isocline) and an empty region (i.e., the region below the isocline). The same feature does not hold for a non-nested network (right panel).

One of the most popular algorithms to quantify the degree of nestedness of a given network is the *Nestedness Temperature Calculator* [5]. Introduced by Atmar and Patterson in 1993 [5], the algorithm first determines an isocline of perfect nestedness by defining a perfectly nested adjacency matrix with the same number of links as the original matrix. Then, it seeks to find the ranking of rows and columns that minimizes the average distance ("temperature" [5]) of observed "unexpected" matrix elements from the isocline of perfect nestedness – the Unexpected matrix elements are those that are different from the corresponding ones in the perfectly nested matrix. While the original Nestedness Temperature Calculator (NTC) by Atmar and Patterson [5] has been widely used in ecology [6], it exhibits some shortcomings that have been later overcome by the BINMATNEST algorithm [22]. BINMATNEST minimizes nestedness temperature through a genetic algorithm that confers higher chance to reproduce upon lower-temperature orderings [22]. The optimal matrices by BINMATNEST tend to exhibit substantially lower temperature that those ranked by the NTC [22], which is why BINMATNEST can be considered as the state-of-the-art approach for nestedness temperature minimization in ecology.

Here, we explore an alternative approach to nestedness temperature minimization inspired by the recent Economic Complexity literature [23,24]. Originally introduced to rank countries and products in the country-product export network [23], the fitness-complexity algorithm ranks the countries and products in such a way that the resulting adjacency matrix exhibits a (typically imperfect) upper-triangular shape [23–26]. In World Trade, this suggests that the most competitive countries tend to diversify their export baskets, whereas the most sophisticated products can be only fabricated by the most competitive countries [23,24]. The country score produced by the algorithm, referred to as country fitness, is positively correlated with country GDPpc [23,24]. Importantly, deviations from the linear-regressed trend are highly informative about the future economic development of the country [27,28], resulting in GDP predictions often more accurate than those by the International Monetary Fund [29,30].

The fact that matrices sorted according to the fitness-complexity algorithm have a neater upper-triangular shape than those sorted by degree suggests that the algorithm might be competitive with algorithms typically adopted in ecology for nestedness temperature minimization [31]. The main goal of this article is to extensively compare the fitness-complexity algorithm and BINMATNEST according to their ability to minimize nestedness temperature. To this end, we analyse 142 mutualistic networks from http://www.web-of-life.es/. We compare the nestedness temperature of the matrices as ranked by BINMATNEST with those of the same matrices as ranked by the fitness-complexity algorithm.

We find that the fitness-complexity algorithm generates sorted matrices that exhibit a lower temperature than the optimal matrices by BINMATNEST for the 66.9% of the analysed networks. The only matrices where BINMATNEST outperforms substantially the fitness-complexity algorithm are low-size and high-density ones. Our findings suggest that while originally introduced as a ranking algorithm in economic production networks, the fitness-complexity algorithm has the potential to become a standard tool for nestedness detection in complex networks.

2. Materials and Methods

This paper focuses on binary bipartite networks. We label row-nodes and column-nodes through Latin ($i \in \{1, \ldots, N\}$) and Greek ($\alpha \in \{1, \ldots, M\}$) letters, respectively. The total number of row-nodes and column-nodes is denoted as N and M, respectively, whereas the total number of links is denoted as L. The network's adjacency matrix is denoted as A: its element $A_{i\alpha}$ is equal to one ("filled" element) if link (i, α) is observed, zero ("empty" element) otherwise. The density Φ of the network is defined as $\Phi = L/(MN)$.

2.1. Nestedness temperature minimization (NTM) problem

Nestedness temperature is determined through three steps: isocline determination, node ranking, and temperature calculation. We provide below the details of the three steps, and state the NTM problem.

First, to compute the nestedness temperature of a given matrix, one needs to determine its *isocline of perfect nestedness*. In this work, we use the definition provided by Rodríguez-Gironés and Santamaría [22] which overcomes some of the shortcomings of the original geometrical construction by Atmar and Patterson [5]. By rescaling the row and columns labels in such a way that they range from 0 to 1, the isocline is determined through the following shape function [22]

$$f(x;p) = \frac{0.5}{N} + \frac{N-1}{N}\left(1 - \left(1 - \frac{Mx - 0.5}{M-1}\right)^p\right)^{1/p}. \quad (1)$$

The isocline is drawn from $(0.5/M, 0.5/N)$ to $(1 - 0.5/M, 1 - 0.5/N)$. This function depends on a single parameter, p, which is determined by imposing that the area above the curve equals the fill of the matrix Φ.

Second, matrix temperature depends on the order of rows and columns. The *nestedness temperature minimization (NTM) problem* (or, equivalently, the *nestedness maximization problem*) consists in determining the ranking of rows and columns that produces a ranked matrix of minimal temperature T (defined below). The output of this step is therefore a pair of rankings, one for rows and one for columns. Equivalently, we can say that the output of the ranking is a *ranked matrix*. Due to the large number of possible permutations of rows and columns, combinatorial search is infeasible [22], which has motivated ecologists to search for fast ranking methods [5,22,32]. The main goal of this paper is to compare two alternative ranking algorithms, the one adopted by BINMATNEST (details in Section 2.2) and the fitness-complexity algorithm (details in Section 2.3).

Third, for a given network and a given ranking of its row-nodes and column-nodes, one calculates nestedness temperature T as follows. The unexpected elements of the ranked matrix are the the empty elements above and the filled elements below the isocline of perfect nestedness (as determined through Eq. (1)). We denote by $\mathcal{U}$ the set of unexpected elements. For each unexpected element (i, α), one draws a straight line of slope -1 in the adjacency matrix (after having normalized to one the column and row labels, as described above). On this line, one compute the distance $d_{i\alpha}$ of unexpected element (i, α) from the isocline, and the distance $D_{i\alpha}$ between the intersection points of this line with the x-axis

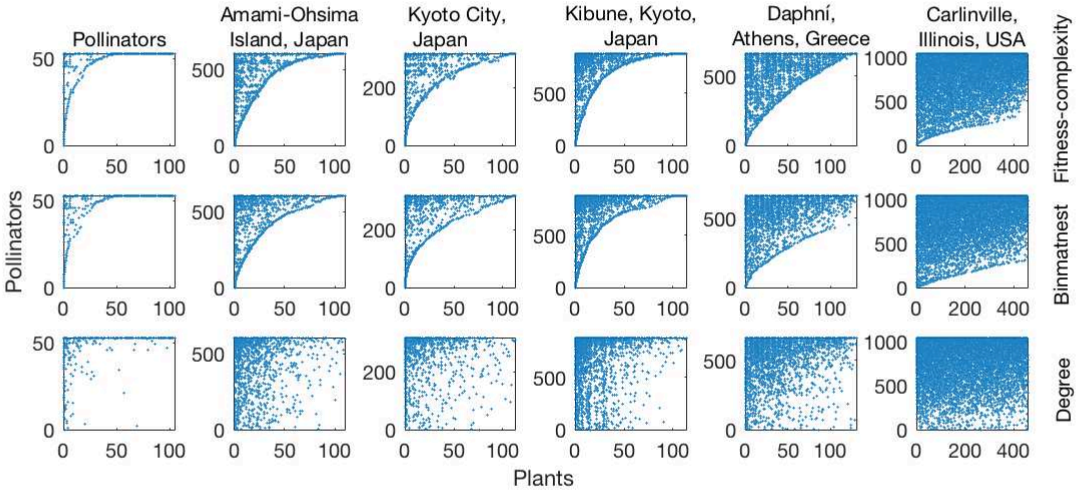

Figure 2. Six empirical mutualistic matrices of different density packed according to three different methods: fitness-complexity algorithm (top row), BINMATNEST (intermediate row), and degree (bottom row). The matrices ranked by fitness-complexity and BINMATNEST are significantly more nested than those ranked by degree.

and y-axis (see Fig. 1 in [22] for an illustration). The total unexpectedness U of the ranked matrix is given by [5,22]

$$U = \frac{1}{N\,M} \sum_{(i,\alpha)\in\mathcal{U}} \left(\frac{d_{i\alpha}}{D_{i\alpha}} \right)^2 . \tag{2}$$

Matrix temperature is defined as $T = 100\,U/U_{max}$, where $U_{max} = 0.04145$ [5,22]. A perfectly nested matrix has zero temperature ("perfect order" [5]), whereas random, noisy matrices have large temperature.

We stress that the key point in our analysis is that the calculation of nestedness temperature T requires a ranked matrix as input: different rankings of rows and columns lead to different matrix temperatures. This allows us to compare different ranking algorithms with respect to the nestedness temperature they produce. We expect the rankings by effective algorithms for NTM to produce ranked matrices that exhibit lower temperature than the ranked matrices by other algorithms.

2.2. Genetic algorithm approach: BINMATNEST (BIN)

The BINMATNEST algorithm [22] adopts a genetic-algorithm approach [33] to the NTM problem. As the computational steps of the ranking algorithm are detailed in [22], we only discuss here the main ideas behind the algorithm. The goal is to find a "solution" of the NTM problem, i.e., the minimal-temperature ranking of the nodes. The algorithm starts with a set of candidate solutions ("chromosomes" in the genetic-algorithm language [33]) – among these solutions, the rankings by degree and by the Nestedness Temperature Calculator by Atmar and Patterson [5]. In each generation, the algorithm considers a well-performing solution, and it generates an "offspring" solution by probabilistically combining elements of the well-performing ranking with elements of a randomly-selected "partner" solution (details in [22]). Besides, the offspring solution can undergo a mutation with a given pre-set probability. The process is iterated for a given number of generations, and the minimal-temperature solution is eventually selected to determine the network nestedness temperature.

The output of the BINMATNEST algorithm is therefore a ranking of the rows and columns that minimizes nestedness temperature T. Importantly, the optimal rankings by BINMATNEST lead to temperature values that are substantially lower than those determined by the widely-used Nestedness

Temperature Calculator [5] – see Figs. 4-5 in [22], for example. Based on those results, BINMATNEST can be considered as the state-of-the-art approach for NTM in ecological networks. In this paper, we implement the BINMATNEST algorithm by using the function nestedrank from the R package bipartite with argument method="binmatnest". This functions gives as output the ranking of row-nodes and column-nodes by the BINMATNEST algorithm.

2.3. Non-linear iterative algorithms: Fitness-Complexity algorithm (FCA)

Originally introduced to rank countries and products in the bipartite country-product export network [23], the fitness-complexity algorithm has been applied to diverse systems including ecological mutualistic networks [31], knowledge production networks [34], food production networks [35]. In its formulation for countries and products [23], the algorithm aims to find a vector of "fitness" scores $\boldsymbol{F} = \{F_i\}$ for countries and "complexity" scores $\boldsymbol{Q} = \{Q_\alpha\}$ for products, respectively. The algorithm starts from a uniform initial condition [23]

$$\begin{aligned} F_i^{(0)} &= 1, \\ Q_\alpha^{(0)} &= 1, \end{aligned} \tag{3}$$

and it subsequently refines the fitness and complexity scores according to the following non-linear iterative equations:

$$\begin{aligned} \tilde{F}_i^{(n)} &= \sum_\alpha A_{i\alpha} Q_\alpha^{(n-1)}, \\ \tilde{Q}_\alpha^{(n)} &= \frac{1}{\sum_i A_{i\alpha} / F_i^{(n-1)}}. \end{aligned} \tag{4}$$

After each iterative step, the scores are normalized by their mean:

$$\begin{aligned} F_i^{(n)} &= \tilde{F}_i^{(n)} / \langle \tilde{F}_i^{(n)} \rangle, \\ Q_\alpha^{(n)} &= \tilde{Q}_\alpha^{(n)} / \langle \tilde{Q}_\alpha^{(n)} \rangle. \end{aligned} \tag{5}$$

Differently from widely-used spectral ranking algorithms (see [28] for a review), the second line of Eq. (4) is markedly non-linear. Such non-linearity is motivated by economic-complexity considerations. Empirical evidence indicates indeed that competitive countries tend to diversify their export baskets, which makes it reasonable to quantify the score of a given country as the sum over the scores of its exported products. At the same time, the fact that a product is exported by many countries (in particular, developing countries) suggests that the product might require few productive capabilities to be made and it is unlikely to be a sophisticated one. This motivates the non-linear dependence of product score $\tilde{Q}_\alpha^{(n)}$ on country score $F_i^{(n-1)}$: $\tilde{Q}_\alpha^{(n)}$ is heavily penalized if α is exported by a low-fitness country.

Do the iterations above converge to a unique fixed point? Scholars have found that while the answer is positive, the scores of several nodes can potentially converge to a zero value, which reduces the discriminative power of the ranking based on the fixed point of the map [36]. Besides, this convergence to zero tends to be relatively slow, and it strongly depends on the density and shape of the adjacency matrix [26,36]. To prevent this potential issue, we adopt a convergence criterion based on ranking: we stop the iterations at step n^* if and only if the ranking of countries and products at step n^* is exactly the same as the ranking at step $n^* - 10$, i.e., if no ranking variations occurred in the precedent ten steps. The criterion allows us to stop the algorithm after a finite number of iteration for all the analysed networks.

While we formulated the algorithm for the country-product network, the algorithm can be applied to any bipartite network by replacing "countries" with the system's row-nodes (e.g., animals in

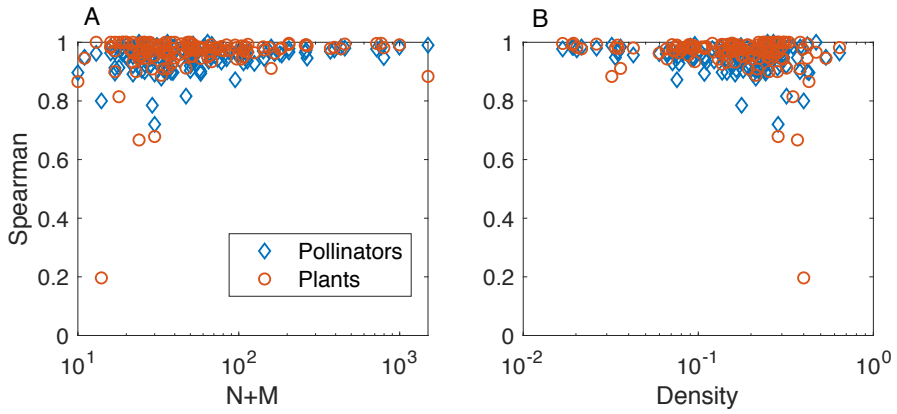

Figure 3. A comparison of the nestedness temperature T_{FC} of the matrices ranked by the FCA with the nestedness temperature T_{BIN} of the optimal matrices found by the BINMATNEST genetic algorithm. The two temperatures are positively correlated (panel A), yet the temperature measured by the fitness-complexity algorithm is lower than that by BINMATNEST for the majority of analysed networks. The only networks where BINMATNEST produces a substantially lower temperature ($T_{FCA}/T_{BIN} > 1$) are characterized by small size $N + M$ (panel B) and high density Φ (panel C).

mutualistic networks [31]) and "products" with the system's column-nodes (e.g., plants). In this paper, we apply it to the mutualistic networks: the fitness score of animal and plant species represents their importance and vulnerability, respectively [31].

3. Results

We analysed the 142 pollination networks provided by The Web of Life (www.web-of-life.es) project. The species are plants (rows) and pollinators (columns) and the type of interaction is Pollination. The main goal of our paper is to compare the FCA and the BINMATNEST algorithm with respect to their performance in the NTM problem. Fig. 2 shows that qualitatively, the matrices produced by the fitness-complexity algorithm are substantially more nested than those produced by ranking the nodes by degree, and their nestedness might be comparable or even larger than that of the matrices ranked by BINMATNEST.

The reason why the FCA produces highly nested structures is that the score of a plant is mostly determined by the least-fit pollinator[1]: a plant that is pollinated by a specialist pollinator is therefore heavily penalized and achieves low complexity score, whereas a plant that is only pollinated by generalists attains a high complexity score. Hence, when sorting plants and pollinators by the FCA, the plants are essentially ranked by the degree of generalization of their least-fit interactors, which naturally results in a nested structure.

We now proceed in a more quantitative fashion by comparing, for all the analysed empirical networks, the temperature values produced by the FCA with those by BINMATNEST. To do this, for the rankings determined by both methods, we determine the corresponding matrix temperature T according to Eq. (2). We find that while the temperature values achieved by the two methods are positively correlated (Fig. 3A), the temperature T_{FCA} by the FCA is lower than the temperature T_{BIN} by BINMATNEST for 66.90% of the networks. The only matrices where the FCA is substantially

[1] Such dependence can be even sharpened by replacing $1/F^{(n)}$ with $(1/F^{(n)})^{\gamma}$ (with $\gamma > 0$) in the dependence of the complexity score on fitness score (second line of Eq. (4)) [25,36], or by defining the complexity of a product directly as the minimum fitness of its interaction partners [26]. However, we do not explore these possibilities here.

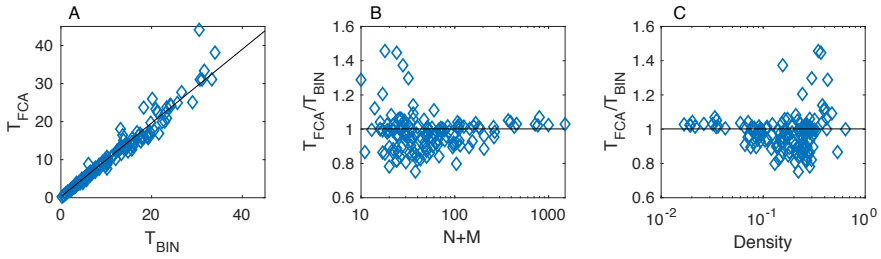

Figure 4. Spearman's rank correlation coefficient ρ between the rankings by BINMATNEST and the fitness-complexity algorithm, for the rankings of pollinators (rhombuses) and plants (circles). Panels A and B represent ρ as a function of size $N + M$ and density Φ, respectively. The two methods produce highly-correlated rankings: the networks where we observe the lowest values of correlation are the small (panel A) and high-density ones (panel B).

outperformed by BINMATNEST are characterized by small size (Fig. 3B) and high density (Fig. 3C), yet these two properties seem necessary but not sufficient for BINMATNEST to outperform the FCA.

Interestingly, among matrices that are found to be "colder" by the FCA, the lowest T_{FCA}/T_{BIN} ratio ($T_{FCA}/T_{BIN} = 0.6664$) was observed in the M_PL_060_13 network ($N = 7, M = 31, L = 48$); in this dataset, $T_{BIN} = 7.9431$ whereas $T_{FCA} = 5.2936$. By contrast, among matrices that are found to be "colder" by BINMATNEST, the highest T_{FCA}/T_{BIN} ratio ($T_{FCA}/T_{BIN} = 1.7740$) was observed in the M_PL_069_03 network ($N = 7, M = 4, L = 15$).

To deepen our understanding of the relation between the rankings by the FCA and BINMATNEST, we study their correlation and how such correlation depends on network properties. The Spearman's correlation coefficient [37] between the rankings by the two methods is positive and relatively high for both plants and pollinators (Fig. 4). Yet, as we have seen in Fig. 3, discrepancies between the two rankings point to a better ability of the FCA to "pack" the matrix in such a way that it displays a nested structure. The networks where we observe the largest discrepancies between the rankings by BINMATNEST and the FCA are the small and high-density ones – for example, the minimal observed correlation for the rankings of pollinators is $\rho = 0.6568$, observed for M_PL_61_39 ($N = 7, M = 23, L = 46$).

4. Discussion

We showed that the fitness-complexity ranking algorithm [23] is a highly effective method to "pack" the adjacency matrix of a given bipartite network in order to maximize its nestedness. In particular, an extensive comparison with BINMATNEST – the state-of-the-art nestedness maximization method in ecology – revealed that the FCA produces ranked matrices with temperature values substantially lower than those of the optimal matrices by BINMATNEST for the majority of analysed datasets. Small, high-density matrices are those where the rankings by the two methods differ the most, and where BINMATNEST has a chance to produce matrices of significantly smaller temperature than those ranked by the fitness-complexity algorithm.

Importantly, the Nestedness Temperature Minimization problem is not only a theoretical one, but it has also implications for the important problem of forecasting of the secondary effects of species' extinctions [31]. More specifically, recent works [25,31] have pointed out that the rankings of active and passive species (countries and products, in World Trade analysis [25]) that result in the most packed matrices are also those that best reproduce the rankings of the nodes according to their structural importance and vulnerability (as determined by numerical simulations of ranking-based targeted attacks to the network). Maximizing nestedness is therefore highly informative on the structural importance of active species and vulnerability of passive species.

Finally, recent literature has reinterpreted nestedness as a mesoscopic property instead of a macroscopic one [15,38,39]. This means that nestedness can be interpreted not as a hierarchical organization of interactions between all pairs of nodes (as in Fig. 1), but as a property of subcomponents of the network. While our results show that the fitness-complexity algorithm can be used as a nestedness detection tool, whether it can be exploited (and arguably, generalized) to detect network compartments that exhibit an internal nested topology remains an intriguing open question.

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Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

The following abbreviations are used in this manuscript:

BIN	BINMATNEST algorithm
NTC	Nestedness Temperature Calculator
NTM	Nestedness Temperature Minimization
FCA	Fitness-Complexity algorithm

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